

Evolution of Thermal Sensitivity in Changing and Variable Climates

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adaptation, environmental exposure, organismal sensitivity, plasticity, thermal performance curve

Abstract

Evolutionary adaptation to temperature and climate depends on both the extent to which organisms experience spatial and temporal environmental variation (exposure) and how responsive they are to the environmental variation (sensitivity). Theoretical models and experiments suggesting substantial potential for thermal adaptation have largely omitted realistic environmental variation. Environmental variation can drive fluctuations in selection that slow adaptive evolution. We review how carefully filtering environmental conditions based on how organisms experience their environment and further considering organismal sensitivity can improve predictions of thermal adaptation. We contrast taxa differing in exposure and sensitivity. Plasticity can increase the rate of evolutionary adaptation in taxa exposed to pronounced environmental variation. However, forms of plasticity that severely limit exposure, such as behavioral thermoregulation and phenological shifts, can hinder thermal adaptation. Despite examples of rapid thermal adaptation, experimental studies often reveal evolutionary constraints. Further investigating these constraints and issues of timescale and thermal history are needed to predict evolutionary adaptation and, consequently, population persistence in changing and variable environments.

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Thermal performance curve (TPC): continuous reaction norms that describe how organismal performance varies with body temperature

1. INTRODUCTION

We review the progress and promise in examining organismal thermal sensitivity to understand ecological and evolutionary responses to changing and variable environments. Since the initial reviews (Huey & Kingsolver 1989, Huey & Slatkin 1976), studies of organismal thermal sensitivity have rapidly accelerated with the pressing applied need to predict ecological and evolutionary responses to environmental change. Acceleration has been particularly rapid since the publication of studies suggesting that predicting environmental change responses requires considering organismal sensitivity to change in addition to the magnitude of environmental change. These studies have pointed out that the evolution of thermal specialization in constant tropical environments could lead to more severe fitness impacts from climate change in the tropics despite a lesser magnitude of climate change there (Deutsch et al. 2008). Subsequent publications have pointed out that exposure to climate change also warrants careful attention: The larger magnitude of thermal variation in temperate areas may lead to similar climate change impacts across latitude despite the broader thermal tolerance prevalent outside the tropics (Kingsolver et al. 2013, Vasseur et al. 2014). Environmental exposure encompasses the environmental variation experienced both currently and as a result of climate change. However, organisms can buffer thermal variation via behavior and temporal shifts (Huey et al. 2012, Woods et al. 2015).

The need to consider both environmental exposure and organismal sensitivity is reflected in broader frameworks for predicting the vulnerability of species and biodiversity to climate change (Williams et al. 2008). Such vulnerability frameworks have been widely invoked and applied (Pacifi et al. 2015). Yet, vulnerability predictions for both real and simulated species differ among frameworks and exhibit poor predictive ability (Wheatley et al. 2017). More broadly, species' traits are generally weak predictors of species' responses to recent climate change (MacLean & Beissinger 2017), and correlative distribution models exhibit mixed performance (Maguire et al. 2015). Incorporating the mechanisms by which species respond to environmental change can improve predictive capacity (Huey et al. 2012), but we lack general frameworks for doing so, and the data requirements of mechanistic models can be prohibitive (Urban et al. 2016).

Here, we focus on the evolution of thermal sensitivity in variable environments to explore the mechanisms by which environmental exposure and organismal sensitivity mediate responses to environmental change. Most relevant research is on thermal sensitivity, but the concepts are broadly applicable to other environmental conditions. Recognition of the biological implications of environmental variability and acute extremes is advancing rapidly (Vasseur et al. 2014). Nonlinear thermal responses mean that the mean of performance at variable temperatures does not equal performance at the mean temperature [i.e., Jensen's inequality (Dowd et al. 2015)]. Recent research points to the importance of characterizing the spatial and temporal environmental variation experienced by the organism as well as organismal responses to the variation, including plasticity. We review insights from well-studied taxonomic groups (insects, lizards, plants, intertidal invertebrates, and microbes) with contrasting environmental exposures and organismal sensitivities.

1.1. Theoretical Insight into Evolutionary Responses to Environmental Variation

Theoretical models of the evolution of thermal sensitivity often invoke thermal performance curves (TPCs) (**Figure 1a**), unimodal relationships that describe performance as a function of body temperature (Huey & Kingsolver 1989, Huey & Slatkin 1976). Initial evolutionary models implemented normal curves (Lynch & Gabriel 1987), but subsequent models incorporated the increased empirical realism of left-skewed curves (Gilchrist 1995). Optimality modelling studies have implemented various forms of environmental, phenotypic, and fitness functions to investigate

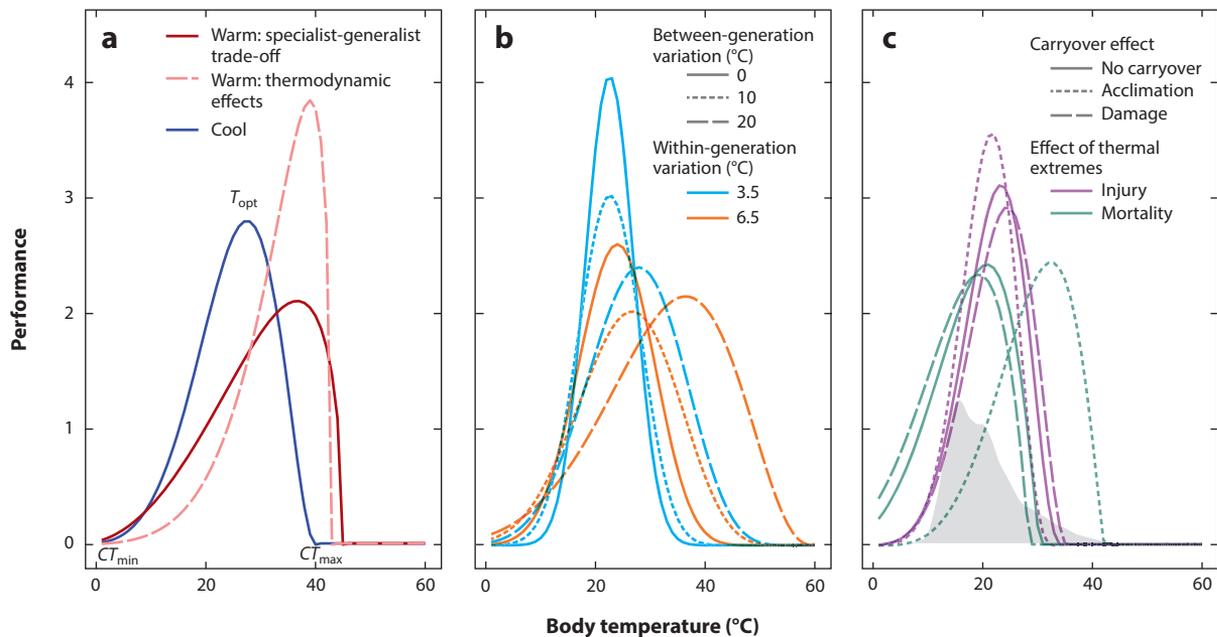


Figure 1

Theoretical insight into the evolution of thermal performance curves (TPCs) in changing and variable environments. (a) A TPC is defined by the lower and upper thermal limits for performance (CT_{\min} and CT_{\max}) and the temperature corresponding to optimum performance (T_{opt}). Two contrasting constraints are assumed to apply to evolution in a warmer environment: Under a specialist-generalist trade-off, the area under the TPC remains fixed, or in the presence of a thermodynamic effect (where hotter is better), the increased rates of biochemical processes at warmer temperatures expand the area under the TPC. (b) Selection for thermal specialization is frequent, but high between-generation environmental variation can select for thermal generalists (Gilchrist 1995). Including thermodynamic effects selects for thermal optima that exceed mean body temperatures, particularly when there is high environmental variation within generations (Asbury & Angilletta 2010). We depict optimal TPCs for scenarios that vary the between-generation (seasonal variation in daily mean temperatures) and within-generation (relative magnitudes of daily temperature variation) environmental variation (Asbury & Angilletta 2010). (c) A quantitative genetic model suggests that whether thermal extremes (above CT_{\max}) cause sublethal performance reductions (injury) or mortality influences the evolution of thermal sensitivity. Evolutionary responses also depend on whether the impact of each subsequent thermal extreme declines (beneficial acclimation) or intensifies (cumulative damage) (Williams et al. 2016). The temperature distribution used in the model is indicated in gray. Abbreviations: CT_{\min} , critical thermal minimum; CT_{\max} , critical thermal maximum.

evolution of TPCs (reviewed in Angilletta 2009). Most models of TPC evolution rely on quantitative genetic models due to the complex genetics underlying thermal sensitivity (Berger et al. 2013).

Model predictions depend crucially on the assumed genetic and phenotypic constraints. One central assumption has been that there is a trade-off between maximum performance and breadth of performance (the specialist-generalist trade-off) (Levins 1968). However, this assumption has garnered limited empirical support (Angilletta 2009), and stronger support has been found for an alternative assumption that the area under the TPC increases at warmer optimal temperatures (thermodynamic effects, summarized as hotter is better) (Angilletta et al. 2010) (**Figure 1a**).

Another related and key assumption in modelling the evolution of thermal sensitivity concerns whether performance primarily influences survival or fecundity and thus how performance aggregates over time to determine fitness (Levins 1968). Predictions differ depending on whether models assume that fitness for a generation is the product (Lynch & Gabriel 1987) or sum (Gilchrist 1995) of performance over time within a generation. Assuming multiplicative performance over time within a generation favors the evolution of thermal generalists. These

Quantitative genetic models: models assuming continuously varying phenotypes that are influenced by many genetic loci

Thermal optima: the body temperature corresponding to maximal organismal performance

Developmental plasticity: nonreversible changes to phenotype due to the environment experienced during early development

assumptions also highlight the importance of the timescale of environmental variation relative to generation length (Gilchrist 1995). Multiplicative integration is also appropriate when performance varies substantially across life cycles, as occurs in plants with rapid early growth. Subsequent models have separately considered the contributions of fecundity (additive) and survival (multiplicative) to fitness to further explore how thermal heterogeneity mediates the evolution of thermal sensitivity (see Section 3.1.2).

The high fitness that specialists achieve when environmental conditions align with their thermal adaptation selects for specialists in most scenarios with within- and between-generation environmental variation (Gilchrist 1995). High between-generation environmental variation can select for thermal generalists, particularly when the TPC influences survival. Thermodynamic effects can select for thermal optima that exceed mean body temperatures, particularly when there is high environmental variation within generations (Asbury & Angilletta 2010) (**Figure 1b**). This dynamic, along with the performance costs of body temperatures exceeding thermal optima (Martin & Huey 2008), aligns with observations of thermal optima exceeding mean environmental temperatures. A complementary eco-evolutionary model, parameterized for insects, integrates quantitative genetic models of TPC evolution with stage-structured population dynamics (Amarasekare & Johnson 2017). Consistent with Jensen's inequality, exposure to large seasonal fluctuations results in the evolution of broad TPCs with thermal optima exceeding mean body temperatures. Thermal specialization with thermal optima matching mean body temperatures evolves under exposure to weak seasonal fluctuations (Amarasekare & Johnson 2017).

Delineating appropriate timescales is a central conceptual problem for TPCs. TPCs were initially envisioned as indicating acute performance (Huey & Slatkin 1976) but have been applied and measured across timescales including long-term growth and fitness (Sinclair et al. 2016). The need to predict the performance and fitness implications of temperature variation at scales ranging from short-term extremes to seasons presents a challenge for the use of TPCs (Rezende et al. 2020). Kingsolver & Woods (2016) constructed a model illustrating how the duration of thermal exposure alters growth rates of ectotherms. They integrated a TPC for energy gain (ingestion rate) with the energy costs of organisms expressing costly heat shock proteins. They assume the expression of heat shock proteins increases asymptotically with increases in both temperature and duration of the thermal stress. The model reproduces empirical findings that juvenile growth rates and optimal temperatures for performance decline as the duration of thermal exposure increases and that temperature fluctuations can alter growth rates. Further incorporating temporal dynamics in TPCs is a primary future direction for the study of TPC evolution.

A related question concerns whether acute thermal extremes influence the evolution of TPCs. Quantitative genetic models demonstrate that even rare thermal extremes can influence the evolution of TPCs (Buckley & Huey 2016). The evolutionary implications of extremes are particularly apparent when the extremes cause mortality or damage and when organisms are unable to use behavior to reduce exposure to extremes. Developmental plasticity, acclimation, and behavior can weaken the selection associated with thermal extremes (Huey et al. 2012, Williams et al. 2016) (**Figure 1c**).

Evolutionary strategies for responding to seasonality and other timescales of environmental variation that shape TPCs include the maintenance of genetic polymorphism, phenotypic plasticity, and bet-hedging (reviewed in Williams et al. 2017). Unpredictable environmental variation can result in the evolution of bet-hedging, whereby a single genotype either produces multiple, narrow TPCs or a single broad TPC.

Phenotypic plasticity and its associated costs can substantially influence the evolution of TPCs in response to environmental variation and change (Kelly 2019, Sgrò et al. 2016). Theoretical models show that plasticity can interact with evolution via two opposing mechanisms: Plasticity

can alternatively slow evolution by buffering selection or facilitate evolution by maintaining genetic variance and population viability (Chevin et al. 2010). Populations and species from more variable environments tend to exhibit more plasticity, but genetic variation may not be sufficiently high or strongly expressed to influence responses to environmental extremes (Chevin & Hoffmann 2017).

1.2. Empirical Patterns of Thermal Sensitivity and Evolutionary Potential

Data characterizing TPCs are accumulating rapidly, but most address critical thermal minima and maxima, CT_{\min} and CT_{\max} , which are the thermal limits of performance that define the x -intercepts of TPCs (Bennett et al. 2018). They are readily measured for many organisms but subject to measurement errors based on methodology. One resolution to the measurement error problem is to develop relationships describing how the duration of exposure influences thermal tolerance estimates (Kingsolver & Umhauer 2018, Rezende et al. 2014). The biological significance of critical thermal limits, and whether they indicate thermal limits of fitness, is unclear (Kingsolver et al. 2013, Sinclair et al. 2016). However, accounting for the effect of exposure duration on thermal tolerance has successfully predicted seasonal patterns of *Drosophila* mortality (Rezende et al. 2020). TPCs can vary systematically across performance traits and levels of biological organization, with TPC breadth tending to decline with aggregation from physiological processes to organismal performance to fitness (Rezende & Bozinovic 2019). For example, the TPC breadth of *Drosophila* fertility is substantially narrower than that for survival, and that for development is slightly narrower again (Williams et al. 2016), and lizard digestion is more thermally constrained than sprint speed (Angilletta et al. 2002).

The most comprehensive compilation of thermal tolerance—the GlobTherm database (Bennett et al. 2018)—which contains data for over 2,000 ectothermic species, is an important resource for comparing TPCs across diverse taxa and habitats. For terrestrial ectotherms, heat tolerance (CT_{\max}) declines slightly with increasing (absolute) latitude and is constant across elevation (Sunday et al. 2019). Heat tolerance declines more rapidly with latitude for aquatic ectotherms, perhaps due to reduced opportunities for environmental buffering. Cold tolerance (CT_{\min}) declines steeply with latitude across ectothermic taxa and with elevation for terrestrial ectotherms (Sunday et al. 2019). Although clines in thermal tolerance generally correspond to clines in climate means and seasonality, divergences provide insight into biological factors influencing TPC evolution. For example, many temperate lizards have higher thermal tolerances than tropical lizards due to their occupancy of relatively open habitats and basking behavior (Huey et al. 2009). Although analyses of thermal tolerance have been focused on animals, plants exhibit similar clines with steeper latitudinal clines in cold tolerance than heat tolerance (Lancaster & Humphreys 2020).

Many fewer estimates are available for the optimal temperature for performance, T_{opt} , because measurement requires estimating performance at multiple constant temperatures. However, T_{opt} is central to understanding fitness in variable environments and the focus of theoretical models. The potential for T_{opt} to evolve relative to thermal limits is a central, unknown factor. Evolutionary potential indicates the capacity for phenotypic evolution in response to environmental change, whereas evolutionary response refers to observed phenotypic evolution. Populations with more genetic variation and more conducive genetic architecture in fitness-related phenotypes have greater evolutionary potential. Evolutionary potential can be measured using quantitative genetic breeding experiments, common gardens or reciprocal transplants, experimental evolution, historical resurveys, and resurrection experiments.

A recent literature survey across taxa found greater evolutionary potential for TPC extremes than interiors (Logan & Cox 2020). Across studies, heritability was moderate for CT_{\min} (0.27 and

Critical thermal minima and maxima: the lower and upper thermal limits for organismal performance

0.28 for broad- and narrow-sense heritability, respectively) and CT_{\max} (0.33 and 0.21 for broad- and narrow-sense heritability, respectively). The very few studies that addressed other TPC traits (maximum performance, performance breadth, T_{opt}) found low heritability, but the greater measurement error of these traits may alter heritability estimates. The studies found evidence of both specialist-generalist trade-offs (87% of studies) and thermodynamic effects (67% of studies). Contrary to previous findings of limited phenotypic plasticity in thermal tolerance (Gunderson & Stillman 2015), the survey found substantial plasticity in gene expression associated with exposure to acute thermal stress (Logan & Cox 2020). Resolving the evolutionary potential of thermal sensitivity and the role of plasticity is an important research direction for understanding responses to climate variability and change.

The ability of TPCs to represent physiological processes and their utility in predicting responses to environmental variation and change are generally limited by assumptions, including that acute (e.g., locomotion) TPCs can predict fitness (Kingsolver & Woods 2016), that TPCs are constant across fitness components and life stages (Kingsolver et al. 2011), that time-dependent responses to thermal variability (e.g., compensatory responses) can be omitted (Huey et al. 2012; Sinclair et al. 2016; Williams et al. 2016, 2017), and that body temperatures equal air temperatures (Huey et al. 2012). Issues that need to be addressed to improve the utility of TPCs have recently been reviewed by Sinclair et al. (2016).

2. MECHANISMS MEDIATING THE EVOLUTION OF THERMAL SENSITIVITY

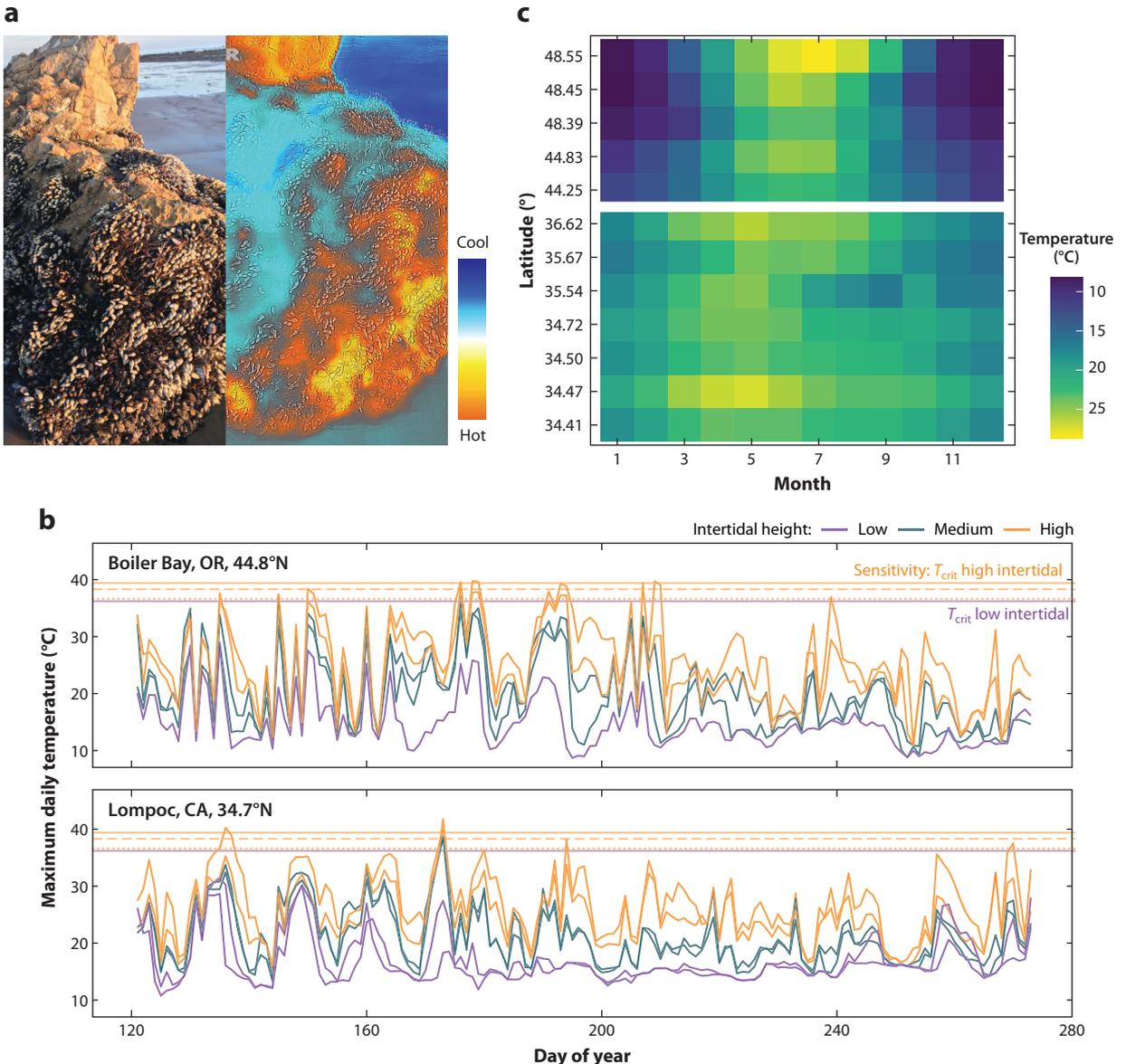
Exposure refers to the extent of climate change and variability experienced by an organism (**Figure 2; Table 1**). Both abiotic and biotic processes alter how organisms experience their environment. Accounting for these processes is essential to characterizing selection on TPCs (Helmuth et al. 2010). Many studies of TPC evolution in ectotherms assume that their body temperatures are equal to air temperatures, often measured by weather stations far above where the organisms live. Operative temperatures, the equilibrium body temperature of a particular organism in a specific microenvironment, can differ from air temperature by tens of degrees Celsius and should be the basis of considering TPC evolution (Sinclair et al. 2016, Sunday et al. 2014). Exposure to solar and thermal radiation is the major factor driving body temperatures to depart from environmental temperatures, but ground temperatures and wind speeds also drive departures (Kearney et al. 2009, Sunday et al. 2014). Biophysical models are increasingly available to translate environmental conditions into operative temperatures (Buckley et al. 2018, Kearney & Porter 2020). Operative temperature estimates should include variation at multiple timescales as well as climate change and the ways in which organisms use behavior to buffer the variation (Huey et al. 2012). The potential for multiple environmental stressors to interact is an important component of exposure (Gunderson et al. 2016).

Microclimate variability both vertically [boundary layer conditions and vertical profiles (Kearney & Porter 2020)] and horizontally [e.g., across habitats (Pincebourde et al. 2016)] can dramatically influence exposure. In an exceptionally local demonstration of microclimate variability (Kaspari et al. 2015), the size of ants determines whether the boundary layer buffers thermal exposure, influencing the evolution of TPCs. The ants' canopy position also influences environmental exposure and TPC evolution. In another fine-scale example, Pincebourde and Casas (2019) demonstrated substantial microclimatic variations at the leaf scale and found that whether herbivore feeding increased or decreased leaf transpiration substantially influences the incidence of thermal stress.

Table 1 Mechanisms of environmental exposure and organismal sensitivity (see text for examples with references)

Element	Components	Aspects	Examples
<p>Exposure: The extent of climate variability and change experienced by an organism. Depends on location, habitat, timing, and behavior</p>	Abiotic components	Microhabitat variability	Small scale microhabitat variability including slope and aspect shape plant exposure
		Temporal variability (diurnal, short-term, seasonal, interannual)	Organisms such as microbes integrate responses to acute extremes and chronic environmental conditions
		Interactions of multiple stressors	Intertidal marine organisms are exposed to dynamic interactions of stressors including temperature, solar radiation, acidity, and desiccation
		Environmental novelty	Differential shifts in temperature and moisture availability are exposing plants to novel environments
	Biotic components	Behavioral buffering (thermoregulation, geographic range and phenological shifts)	Effective behavioral thermoregulation shapes the environmental exposure of lizards
		Seasonal timing	For organisms with multiple annual generations, such as many insects, generations can experience distinct environmental conditions
		Complex life cycles	Intertidal marine organisms can experience dramatically different conditions as pelagic larvae and sessile adults
<p>Sensitivity: The responsiveness to a given amount of climate change and variability. Depends on organismal factors including physiology, life history, and genetics</p>	Components	Physiological traits	Digestion is often the most thermally sensitive component of energy acquisition in lizards
		Developmental plasticity	Development plasticity in insect coloration can buffer sensitivity to environmental variation
		Reversible plasticity	Induced heat shock responses in intertidal invertebrates can reduce organismal sensitivity
		Life history	Early life stages of plants can be particularly sensitive to thermal stress
		Genetic structure	Genetic trade-offs between adaptation and plasticity shape the sensitivity of intertidal invertebrates

Behavior and other biotic buffers determine an organism's ability to select microclimates and evade thermal stress (Huey et al. 2012). Thermoregulatory behavior, primarily regulating time of activity and selecting between sunny and shady microhabitats, is necessary for many organisms to avoid thermal stress (Kearney et al. 2009, Sunday et al. 2014). Organisms shift seasonal timing and thus exposure via changes in both behavior and developmental rates. An interesting dynamic is that climate warming can increase development rates and shift phenology earlier, which can expose organisms to variable, early-season conditions with consequences such as frost damage (Inouye 2008). Environmental exposure also varies across complex life cycles (Kingsolver et al.



(Caption appears on following page)

Figure 2 (Figure appears on preceding page)

Mussel biomimetics reveal how thermal exposure and sensitivity vary across the intertidal zone along the US west coast (data from Helmuth et al. 2016). (a) A paired visual and thermal image of an intertidal rock covered in mussels and barnacles illustrates how thermal exposure varies with aspect and fine-scale structure from cool (blue) to hot (orange). (b) A mussel's exposure to thermal stress depends on its geographic location, intertidal height (low, purple; medium, green; high, orange), and microhabitat variability (indicated by multiple lines of a single color) for an exemplar year. We use the critical temperature (T_{crit}) at which mussel heart rate precipitously declines to explore patterns of thermal sensitivity (data from Moyon et al. 2019). We depict T_{crit} values for a single California population of *Mytilus californianus* but note the values are approximate due to geographic differences in T_{crit} (Logan et al. 2012). T_{crit} varies among mussels from low (horizontal purple line) and high (horizontal orange lines) positions in the intertidal that were exposed to fast heating rates (solid lines). Heating rates (an aspect of exposure) vary with shelter from waves and intertidal height. For the high intertidal mussels alone, T_{crit} varies with heating rate (the dotted line indicates a slow heating rate) (Moyon et al. 2019). Acclimation to high, variable temperatures was found to be gradually lost; the dashed line represents the T_{crit} of high intertidal mussels after 8 weeks in benign conditions (Moyon et al. 2020). The T_{crit} differences (compare the horizontal orange lines) reflect differences in sensitivity due to plasticity. Thermal exposure and sensitivity jointly determine the incidence of thermally stressful conditions exceeding T_{crit} . (c) Seasonal patterns of thermal exposure (monthly means of maximum mussel daily temperatures within a site) depart from smooth latitudinal clines. Elevated thermal exposure results from the coincidence of high air temperatures and high solar radiation during midday low tides that tend to occur in summer at the Northern sites. Panel c adapted from Buckley et al. (2018).

2011). For example, pelagic juvenile stages of marine organisms experience drastically different environmental conditions than sessile adults.

Emerging research is revealing that thermal tolerance can be shaped by associated organisms. The best known example of this phenomenon is algal symbionts shaping the thermal tolerance of corals (Berkelmans & Van Oppen 2006). But bacterial symbionts can alter the thermal tolerance of hosts including insects (Wernegreen 2012). For example, a point mutation in the *Buchnera* bacterium alters aphid thermal tolerance by preventing the expression of heat-shock proteins (Dunbar et al. 2007). Pathogens and parasites likewise affect host thermal tolerance (Greenspan et al. 2017).

Organismal sensitivity refers to how responsive performance and fitness components are to a given amount of environmental change based on physiology, life history, and genetics (**Figure 2**; **Table 1**). The importance of considering sensitivity is clear from studies of how thermal specialization determines climate change impacts (Deutsch et al. 2008). The ability of an organism to mount either a constituent or induced stress response is another key component of sensitivity (Somero 2010). Both developmental and reversible plasticity can decrease sensitivity (Sgrò et al. 2016). Evolutionary potential is sometimes considered a component of organismal sensitivity (reviewed by Catullo et al. 2019). We omit it here because our goal is to investigate how environmental exposure and organismal sensitivity influence TPC evolution. We note that TPCs are both a component of and shaped by sensitivity.

3. TAXONOMIC CASE STUDIES

Most studies of evolution of thermal sensitivity have focused on a few groups of ectothermic taxa. We illustrate how environmental exposure and organismal sensitivity mediate the evolution of thermal sensitivity by examining well-studied taxa that differ in these elements of vulnerability (for a taxonomic comparison, see **Table 2**). We highlight focal studies that examine the interplay of exposure and sensitivity.

3.1. Insects

Rates of insect growth, development, performance, and fitness are highly temperature dependent, augmenting organismal sensitivity (Hodkinson 2005). Rapid life cycles and the occurrence of diapause shape environmental exposure. Complex life cycles with stages differing in mobility and habitat further shape environmental exposure (Kingsolver et al. 2011).

Reversible plasticity: reversible changes to phenotype in response to environmental conditions that happen within a generation

Table 2 Comparing taxonomic groups reveals key differences in environmental exposure, organismal sensitivity, and the evolutionary potential of thermal sensitivity (see text for references)

Organism	Exposure	Sensitivity	Evolutionary potential
 <p>Insects</p>	<p>Small size and limited mobility of some life stages leads insects to experience pronounced microclimate variability (e.g., sunny and shady leaves), but thermoregulation is common among adults</p> <p>Rapid development interspersed with long periods of inactivity shapes temporal variability</p> <p>Developmental processes are often sensitive to both temperature and photoperiod</p> <p>Complex life cycles and seasonal timing strongly influence exposure</p>	<p>Growth, development, and fitness are highly temperature sensitive</p> <p>Pronounced developmental and reversible plasticity enables responses to seasonality</p> <p>Climate means and variability tend to influence distinct fitness components (i.e., fecundity and survival, respectively)</p>	<p>Climate fluctuations can slow selection, but plasticity can buffer variation</p> <p>Experimental evolution studies reveal substantial evolutionary potential, but environmental variation may limit selection in the wild</p> <p>Genetic constraints and environmental variability limit potential to evolve heat resistance</p>
 <p>Lizards</p>	<p>Lizards effectively use thermoregulation to select microhabitats, but temporal variability constrains their activity timing</p> <p>Burrows or shelters often limit environmental exposure</p> <p>Shifts in development time and activity shape seasonal timing</p>	<p>Thermal constraints on activity time and performance strongly influence fitness</p> <p>The thermal dependence of rates of energy acquisition and use are an important component of sensitivity</p> <p>Limited evidence for developmental or reversible plasticity, but physiological traits vary across their life cycle</p>	<p>Documented selection on thermal sensitivity, but low heritability of thermal traits limits evolutionary responses</p> <p>Thermoregulatory behavior buffers selection and evolution</p>
 <p>Plants</p>	<p>Interactions of temperature, moisture, and nutrient availability can produce complex patterns of spatial and temporal exposure</p> <p>Drought is a key acute exposure</p> <p>Small scale microhabitat variability including slope and aspect shape exposure due to limited buffering capacity</p> <p>Complex life cycles shape temporal exposure.</p>	<p>Sensitive to both chronic (e.g., growing degree days) and acute (e.g., water stress) conditions</p> <p>Developmental and reversible plasticity shape sensitivity including genetic stress responses</p> <p>Life history mediates sensitivity</p>	<p>Seasonal exposure can alter selection</p> <p>Pronounced plasticity, particularly phenological shifts, can buffer selection and slow evolution</p> <p>Adaptation lags can occur</p> <p>Adaptive potential stronger in response to stressful conditions (e.g., drought)</p>
 <p>Intertidal invertebrates</p>	<p>Complex lifecycles, e.g., pelagic larvae and sessile adults, shape exposure</p> <p>Tidal cycles create complex and pronounced patterns of spatial and temporal variability</p> <p>Strong interactions of stressors including temperature, solar radiation, acidity, and desiccation</p>	<p>Extreme conditions select for pronounced developmental and reversible plasticity including strong genetic stress responses</p> <p>Sensitivity varies across life history</p>	<p>Patterns of environmental variation drive strong selection and can produce trade-offs between adaptation and plasticity</p> <p>Either constituent or induced stress responses can evolve depending on the degree of environmental variation</p> <p>Multiple stressors can alternatively promote and limit evolution</p>
 <p>Microbes</p>	<p>Spatial and temporal environmental variation strongly shape exposure due to rapid and often simple life cycles</p> <p>Strong potential for interactions of multiple stressors and environmental novelty</p> <p>Limited biotic component of exposure, but mixing and dispersal patterns influence exposure</p>	<p>Microbes differ dramatically in their thermal breadth and optima</p> <p>Sometimes pronounced developmental and reversible plasticity including genetic stress responses</p>	<p>Rapid life cycle results in strong evolutionary potential if genetic variation is sufficient</p> <p>Plasticity can facilitate rapid evolution, but the role of environmental variability warrants further consideration</p>

3.1.1. Overview. Rapid evolution of thermal physiology has occurred in laboratory selection experiments for insects with short life cycles such as *Drosophila*, but questions remain about which TPC traits evolve and how relevant laboratory experiments are to nature (for a review, see Hoffmann et al. 2003). Selection on performance at a series of intermediate, constant temperatures led to subtle shifts in thermal tolerance consistent with genetic correlation of TPC traits (Huey

et al. 1991). At higher selection temperatures, flies exhibited slightly higher thermal optima for walking; smaller performance breadths; and greater tolerance to acute, extreme high temperatures (Gilchrist et al. 1997). No evidence of genetic coupling was found for tolerance of low extremes (Gilchrist et al. 1997). Eggs exhibited similar thermal tolerance across selection temperatures.

The literature on *Drosophila* thermal sensitivity and tolerance suggests the importance of evolutionary trade-offs and constraints (Hoffmann et al. 2003). For example, selection for heat tolerance can decrease hardening plasticity and induce trade-offs between basal and induced resistance. Photoperiod and energy reserves can influence thermal sensitivity and plasticity. The genetic bases for TPC evolution are poorly understood even in *Drosophila*, but for a review of the heat shock response responsible for hardening in response to thermal extremes, see Feder & Hofmann (1999).

Overall, laboratory and experimental evolution studies suggest limited capacity for heat resistance to evolve across insects, particularly in the context of variable natural environments (Kellermann & Heerwaarden 2019, but for a review of evolutionary and plastic changes, see Schilthuizen & Kellermann 2014). Breeding experiments on an invasive beetle indicate that critical thermal limits have an additive genetic basis. However, the experiments revealed low heritability of TPC components such as optimum and breadth as well as evidence that genetic correlations constrain TPC evolution (Logan et al. 2020). Nevertheless, rapid evolution of thermal tolerance is observed for some insects such as ants along an urban–rural temperature cline (Diamond et al. 2017).

3.1.2. Case study of *Colias* butterflies. A resurvey project for montane *Colias* butterflies has investigated how exposure and sensitivity shape responses to climate variability and change. A key thermoregulatory trait for these butterflies is wing melanin, which increases the absorptivity of solar radiation and thus body temperature (Watt 1968). Extending a mechanistic modelling framework that incorporates microclimate, heat balance, and demographic models to include evolution and plasticity reveals patterns of selection and evolution consistent with but more complex than the a priori expectation that climate warming would select for lighter wings at low elevation (and thus reduced heat loads) but darker wings at high elevation (to capitalize on warming) (Kingsolver & Buckley 2017). The models predict initial darkening at high elevation that leads to evolutionary lags that ultimately reduce fitness as the climate warms (Buckley & Kingsolver 2019).

A prominent feature of the models is how seasonal and annual variation in climate causes the strength and direction of selection to fluctuate, slowing evolution (Kingsolver & Buckley 2017). The models suggest that plasticity in wing absorptivity can facilitate evolution, particularly at lower elevations with long seasons, by reducing temporal variation in the strength and direction of evolutionary selection (Kingsolver & Buckley 2017). Phenological shifts (e.g., timing of maturation) caused by environmental effects on developmental rate can also reduce variation in selection (Kingsolver & Buckley 2017).

Examining museum specimens of *Colias* collected over the past half century (MacLean et al. 2019) generally confirmed model predictions but also highlighted how joint plastic and evolutionary responses can complicate the interpretation of phenotypic shifts. Contrary to model predictions, we detected no evolution of plasticity in wing absorptivity (cued by pupal temperatures), potentially due to genetic constraints that were not accounted for in the model. However, reduced melanization has evolved at short photoperiods over nearly 50 years, consistent with greater increases in spring temperatures (Nielsen & Kingsolver 2020). Feeding experiments with *Colias* larvae in the 1970s and 2010s suggested evolutionary shifts in TPCs have occurred to allow feeding at higher temperatures, associated with an increase in the incidence of warm extremes (Higgins et al. 2014) (**Figure 3a**).

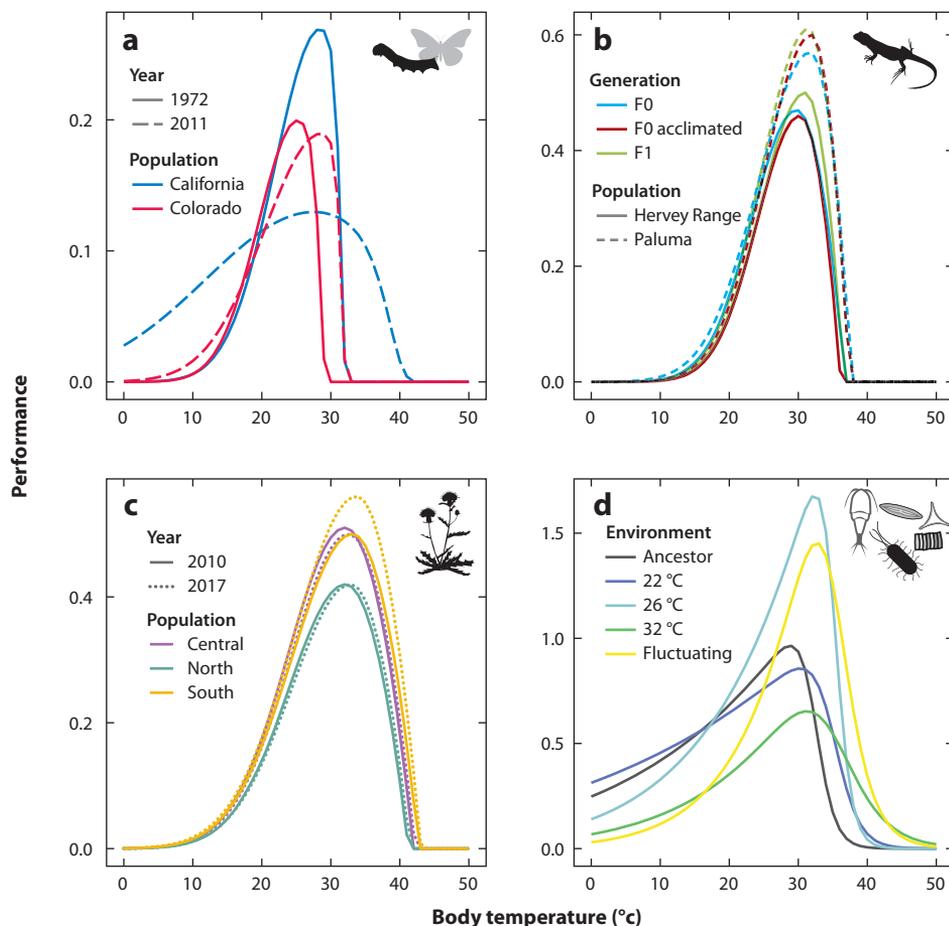


Figure 3

Empirical examples of the plasticity and evolution of TPCs in response to experimental treatments or to environmental change in natural populations. (a) The thermal sensitivity of *Colias* caterpillar feeding has shifted, enabling feeding at warmer temperatures as warm extremes became more frequent over 4 decades. While a Colorado population primarily exhibited a TPC shift, thermal sensitivity broadened for the California population (Higgins et al. 2014). (b) The tropical lizard *Lampropholis coggeri* exhibits TPC variation due primarily to reversible plasticity and adaptation among two populations (Hervey Range and Paluma). TPCs are depicted for field-collected (F0) and lab-acclimated (F0 acclimated) as well as laboratory-reared (F1) lizards (Llewelyn et al. 2018). (c) A resurrection study using *Mimulus* seeds collected from three populations before and after 7 years of warming reveals little TPC adaptation (Wooliver et al. 2020). (d) Experimental evolution of the marine diatom *Thalassiosira pseudonana* reveals slower TPC adaptation in hot (32°C) than in moderate (26°C) or fluctuating (FS: varying between 22 and 32°C) thermal conditions. The ancestor was derived from long-term culture at 22°C (Schaum et al. 2018). Data from original publications and code to plot the TPCs are available at https://github.com/HuckleyLab/TPCevolution_AREE. Abbreviations: FS, fluctuating; TPC, thermal performance curve.

3.2. Lizards

Lizards are a focal taxon for investigating thermal sensitivity and its implications due to the pronounced thermal determination of their rates of energy acquisition and use. TPCs for locomotion have been used as a basis for predicting activity times and energy budgets. Climate warming is

predicted to reduce activity time for species thermally adapted to current environments (Huey et al. 2009). Models predict that reduced activity, particularly during the reproductive season, will elevate extinction risk for many lizard populations (Sinervo et al. 2010).

3.2.1. Overview. Behavioral thermoregulation and its impact on the evolution of thermal sensitivity is particularly important for temperate lizards in exposed habitats (Huey et al. 2009). TPC evolution is likely to be a stronger determinant of climate change responses for lizards in forested habitats, particularly those in the tropics that are already living close to their thermal optima, because they have fewer opportunities for thermoregulation and often have low T_{opt} and CT_{max} (Huey et al. 2009). Indeed, transplanting tropical *Anolis* lizards to a warmer, more thermally variable site resulted in selection for the ability to run at warmer temperatures and across a broader range of temperatures (Logan et al. 2014). However, common garden experiments with lizards from the two sites indicate limited heritability of both TPC components and thermoregulatory behavior (Logan et al. 2018). Together, these results suggest a limited role for TPC evolution in lizards' climate change responses. However, phenotypic, regulatory, and genomic shifts were observed in *Anolis* lizards in response to an extreme cold event (Campbell-Staton et al. 2017): Changes in genomic regions important for functioning in the cold were associated with increased cold resistance for southern populations.

Studies of the rainforest sunskink (*Lampropholis coggeri*) suggest that plasticity plays a larger role in responding to climate variability and change than evolutionary adaptation. Patterns of thermoregulation have resulted in countergradient thermal sensitivity (Catullo et al. 2019). The less plastic response in thermal tolerance in skinks with higher CT_{max} suggests limits to heat tolerance. A more plastic response was observed in skinks from more predictable environments (Phillips et al. 2016). Lab rearing revealed acclimation of thermal sensitivity but not desiccation resistance (Llewelyn et al. 2018) (**Figure 3b**). Conversely, developmental plasticity was limited for thermal sensitivity but more pronounced for desiccation resistance. Heritability was moderate for thermal sensitivity traits ($h^2 < 0.31$) but somewhat higher for desiccation resistance ($h^2 \approx 0.42$) (Llewelyn et al. 2018). Collectively, these studies suggest that plasticity, including behavioral thermoregulation, and low levels of heritability limit evolutionary adaptation of TPCs for lizards.

3.2.2. Case study for *Sceloporus* lizards. Many lizards effectively use behavioral thermoregulation to limit environmental exposure. This behavioral buffering of environmental variation can weaken selection on and slow the evolution of thermal sensitivity (Huey et al. 2012, Logan et al. 2019). Configurations of thermal landscapes in terms of number, size, and spread of shady patches strongly influence how effectively lizards can behaviorally thermoregulate (Sears et al. 2016). For the extensively studied *Sceloporus* lizards, optimality models suggest that the ability of thermoregulatory behavior to buffer selection is consistent with the nearly uniform thermal sensitivity of locomotion across the group's broad geographic distribution (Buckley et al. 2015). The analysis suggests that this behavioral buffering may ultimately confer great sensitivity to climate change as warming proceeds and opportunities for thermoregulation erode. Another form of plasticity that can limit lizards' exposure is nesting-site selection. However, an experiment with *Sceloporus* suggests that nesting plasticity is insufficient to buffer climate change impacts (Telemeco et al. 2017).

Considering differences in thermal sensitivity across lizards' life cycles substantially alters the climate change impacts predicted by mechanistic models. Incorporating the increased thermal sensitivity of embryos as well as the thermal stress associated with hourly fluctuations in soil temperature dramatically increased estimates of fitness loss associated with future climate change (Levy et al. 2015). These life-stage differences interact with environmental exposures to determine

the fitness impacts of phenological shifts (Levy et al. 2016). Longer growing seasons associated with warming can increase rates of growth and development in cold regions. Warming advances the reproductive season but also reduces the survival of embryos and juveniles in warm regions. Stressful summer temperatures may thus offset the benefits of an extended season (Sinervo et al. 2010). Whether lizards reside in cold or warm regions is also expected to alter the energetics of climate change impacts. Climate change may alter lizard energetics primarily through digestion rather than feeding. Declines in energy-assimilation rates with increasing thermal opportunity imply that shifts in energetics with climate warming will be most pronounced in cold regions where thermal opportunity is limited (Levy et al. 2017).

3.3. Plants

The immobility of plants limits behavioral buffering, but some plants effectively use phenological avoidance, dormancy, and leaf cooling. However, expectations that plants would thus be selected for broad thermal sensitivities and phenotypic plasticity have received only limited empirical support (Huey et al. 2002). TPCs for photosynthesis and growth have been extensively documented and are incorporated in vegetation and crop models (Kumarathunge et al. 2019). For example, differences in temperature and CO₂ sensitivity between plants with C₃ and C₄ photosynthesis provide a strong basis for predicting relative responses to climate change (Huang et al. 2001). However, plant TPCs have rarely been linked to natural selection and evolutionary responses to climate variability and change in wild populations.

3.3.1. Overview. There is great potential for linking plant TPCs to fitness and distributions, due to the relative ease of common garden and reciprocal transplant experiments. Indeed, environmental sensitivities revealed by transplant experiments often correspond to range limits (Lee-Yaw et al. 2016). However, common garden experiments in plants have also uncovered adaptational lags whereby warm-adapted populations can exhibit higher fitness than local populations (Wilczek et al. 2014). Genetic correlations and antagonistic selection on multiple plant traits can impede evolutionary responses to climate change (Etterson & Shaw 2001).

We highlight several examples of the value of applying an evolutionary TPC framework to plants. Extensive common gardens for pine seedlings demonstrate strong effects of local adaptation on fitness across environmental gradients and the potential for movement of locally adapted genotypes to shape climate change responses (Aitken et al. 2008). Developmental threshold models can effectively predict phenology, life cycles, and distribution limits (Donoghue 2008). Additionally, TPCs for germination rates suggest that tropical plants may be more at risk from climate change than temperate plants, because they occupy habitats closer to their upper thermal tolerances (Sentinella et al. 2020). An important consideration for plants is that their fitness and distributions are often dually constrained by temperature and moisture, which requires investigating environmental sensitivities beyond temperature (see Section 5).

3.3.2. Case study for *Mimulus* monkeyflowers. Studies with *Mimulus* (monkeyflowers) demonstrate the potential of applying a TPC framework to understand plant responses to environmental variation. The species *Mimulus cardinalis* and *Mimulus lewisii* exhibit survival, growth, and leaf physiology TPCs consistent with their different elevational distributions (Angert 2006). Common garden and reciprocal transplant experiments suggest that trade-offs in thermal sensitivity limit the species' altitudinal distributions (Angert et al. 2008). For geographic ranges, *Mimulus* species that experience greater thermal variation across their ranges exhibit broader thermal tolerances and greater within-population genetic variation in TPCs (Sheth & Angert 2014). Growth

TPCs for 12 populations of *M. cardinalis* suggest specialist-generalist trade-offs. Applying the TPCs to project performance responses to environmental variability and change result in the predictions that thermal optima and breadth shape the magnitude and direction of distribution shifts (Angert et al. 2011).

Resurrection studies have proved a valuable tool for investigating the evolution of environmental sensitivity. Many resurrection studies have focused on droughts because they can impose strong selection. For example, a resurrection study with the annual *Mimulus laciniatus* documented reduced and less variable development time following drought, suggesting the potential for rapid evolution in response to climate extremes (Dickman et al. 2019). In contrast, a resurrection study with the perennial *M. cardinalis* provided only limited evidence for TPC shifts following a 7-year period of record warming (Wooliver et al. 2020) (**Figure 3c**). One southern population evolved a narrow TPC consistent with the observed shift in seasonality. The study provides an important initial demonstration of the limits to rapid adaptation of TPCs, but the focus on seedling growth for a short duration in relatively constant conditions limits inferences regarding TPC evolution in response to climate change. The study should inspire further application of the TPC framework to investigate plant responses to variable and changing environments.

3.4. Rocky Intertidal Invertebrates

Interactions of multiple stressors are likely to be particularly relevant for marine taxa given the confluence of thermal stress and acidification they experience (Gunderson et al. 2016). Patterns of environmental variation depend strongly on depths and currents. In particular, pH variation exhibits no pronounced latitudinal gradient, and the magnitude and frequency of temporal variation differs substantially across locations (Kelly & Hofmann 2013). We focus our review on rocky intertidal invertebrates since extensive experimental work has characterized their exposure and sensitivity. A lack of historic data has limited examples of evolutionary responses to climate change (Reusch 2014).

3.4.1. Overview. Intertidal invertebrates inhabit a highly dynamic environment characterized by relatively constant and moderated conditions when submerged interspersed with intense periods of exposure, often to multiple stressors. Models suggest that rare heat events associated with high air temperatures, intense solar radiation, and low windspeeds can drive the evolution of increased heat tolerance in limpets (Dowd et al. 2015). Extensive measurements of mussel body temperatures demonstrate that intertidal thermal stress occurs as a mosaic rather than latitudinal gradient due to factors such as the coincidence of midday low tides and high solar radiation (**Figure 2**) (Helmuth et al. 2016). Dramatic environmental gradients over short spatial scales in the intertidal highlight environmental heterogeneity. Zonation results from differences in both thermal tolerance and longer-term energy limitations (Somero 2002).

Periodic stressors in the intertidal result in energetic costs associated with heat-shock responses, replacing denatured proteins, restructuring cellular membranes, and altering gene expression (Somero 2002). The extent and frequency of environmental variation influence whether intertidal organisms exhibit constituent or induced responses to thermal extremes (Feder & Hofmann 1999). Heat tolerance and acclimation potential are negatively correlated genetically in some marine taxa (Gunderson & Stillman 2015). Other taxa do not exhibit such trade-offs, but plasticity in thermal tolerance is generally found to have limited capacity to buffer thermal stress (Gunderson & Stillman 2015).

A key component of sensitivity for many intertidal invertebrates is that their life stages vary in mobility and habitat. Early life stages of marine invertebrates are particularly sensitive to warm

extremes (Pandori & Sorte 2019). Genetic differentiation and local adaptation tends to be most pronounced in species that develop locally without the mixing that can occur in species with a planktonic phase (Somero 2002).

3.4.2. Case study of intertidal copepods. A series of experiments on the intertidal copepod *Tigriopus californicus* illustrates how exposure and sensitivity shape the interplay of plasticity and evolution. Populations exhibiting local adaptation to temperature and competition suggest trade-offs between performance at high, stressful temperatures and moderate temperatures (Willett 2010). In contrast to latitudinal gradients in thermal tolerance, within-population variance in thermal tolerance is limited. Consequently, neither acclimation nor strong selection were able to produce the heat tolerance observed in some populations, and a plateauing of heat tolerance suggested that low standing variation limited evolutionary potential (Kelly et al. 2012). Indeed, within-population variation rather than fitness trade-offs seems to limit the evolution of heat tolerance.

Lines selected for increased heat tolerance experienced fitness increases (increased size, fecundity, and starvation resistance) in nonstressful conditions. Other fitness traits responded variably to selection among populations, suggesting different genetic bases for thermal tolerance (Kelly et al. 2013). The evolution of heat tolerance can result in reduced phenotypic and transcriptional plasticity (Kelly et al. 2017; for similar observations in other systems, see Somero 2002). Selection for heat tolerance can reduce fecundity, suggesting an energetic cost to tolerance (Kelly et al. 2016). Competing energetic demands, rather than a shared stress-response pathway, resulted in trade-offs between tolerance of heat and salinity (Kelly et al. 2016). More broadly, the synergistic responses of intertidal organisms to heat and acidification stress suggest physiological trade-offs, often mediated by energetics (Kelly & Hofmann 2013).

3.5. Microbes

Extensive experimental studies of microbes indicate the potential for rapid evolution of thermal sensitivity in response to variable and changing environments and a role for plasticity in facilitating evolution (reviewed by Collins et al. 2019).

3.5.1. Overview. We highlight a small subset of the research and focus on phytoplankton. Despite the extensive research we omit, including excellent work on thermophiles, there is a need to further consider the role of environmental variation and taxonomic variation in plasticity (Schaum et al. 2018). The timescales and temporal autocorrelation of environmental variation can influence the evolution of heat tolerance (Wieczynski et al. 2018). Trade-offs and genetic correlations in TPC evolution have been observed inconsistently, warranting further investigation (Bennett & Lenski 1993).

3.5.1. Case study for phytoplankton. A series of experiments on freshwater algae in both the lab and mesocosms provide insight into the interplay of plasticity and evolution. Populations from more variable environments exhibit more plasticity and evolve more in response to acidification (Schaum & Collins 2014). The role of plasticity in promoting evolution was found to be strongest in fluctuating environmental conditions. Interestingly, the degree of plasticity predicted the extent but not the direction of evolution. Other laboratory experiments have confirmed the potential for rapid evolution of thermal sensitivity. High temperatures were observed to decrease population growth of a freshwater phytoplankton due to respiration rates responding more to temperature

changes than photosynthesis. The plankton evolved tolerance to high temperature via stronger downregulation of respiration relative to photosynthesis (Padfield et al. 2016).

The evolutionary potential of phytoplankton was confirmed by a decade-long outdoor mesocosm experiment that allowed more realistic environmental variation (Schaum et al. 2017). Similar to the previous study, adaptation to warming was observed to occur via increased photosynthetic capacity and a reduced susceptibility to photoinhibition. These shifts resulted in higher temperatures for optimal growth, which increased the plankton's relative growth rates in warm temperatures with the trade-off of lesser relative growth rates at ambient temperatures. Temperature fluctuations between hot and benign conditions facilitated the evolution of heat tolerance in a marine diatom (Schaum et al. 2018) (**Figure 3d**).

4. SUMMARY

While laboratory studies of experimental evolution often suggest substantial evolutionary potential, many such studies are conducted in constant and simplified environments. Field studies reveal that environmental variation can drive fluctuations in selection that slow evolution. More carefully translating environmental conditions into the ways in which organisms experience their environment will help clarify environmental exposure. Consideration of organismal sensitivity is likewise crucial. Important components are phenotypic plasticity and its interplay with evolution. Plasticity tends to facilitate the evolution of thermal sensitivity in taxa that are exposed to pronounced environmental variation, including insects, intertidal invertebrates, and microbes. Forms of plasticity that buffer exposure rather than shift thermal sensitivity can hinder evolution. For example, lizard behavioral thermoregulation and plant phenological shifts can limit thermal stress and slow selection.

While most taxa we considered exhibit cases of local or rapid adaptation of thermal sensitivity, experimental studies often reveal constraints on the evolution of thermal sensitivity. Constraints associated with limited genetic variation, genetic correlations, and trade-offs warrant further investigation. Both theoretical models and more realistic models of TPC evolution for particular taxa provide insight into potential evolutionary responses, but further extending the models to incorporate realistic environmental variation including extremes and evolutionary constraints is needed. Studies using historic data or resurrection approaches are proving particularly valuable in understanding the evolution of thermal sensitivity in variable and changing environments.

TPCs offer a promising means of integrating organismal responses to short-term environmental variability and long-term climate change once issues of time dependence in both measuring and applying TPCs are addressed. Combining distinct TPCs for different fitness-determining processes can help clarify the implications of climate variability and change for demography and population persistence. For example, TPCs for survival tend to be more symmetric and often best reflect responses to acute thermal extremes. TPCs for performance can be applied to estimate activity durations and energetics that reflect aggregate responses to chronic environmental conditions. Appropriately estimating TPCs and applying them to estimate fitness and demographic implications requires considering the exposure and sensitivity of organisms.

5. FUTURE DIRECTIONS

5.1. Striking a Balance Between Realism and Tractability for Future Experimental Work

Increasing recognition of the evolutionary importance of climate variability and extremes is inspiring experiments to move beyond quantifying thermal sensitivity to constant or trending

environmental conditions. How to design experiments that balance realism and tractability is an important consideration. We need to collectively refine the measurement of TPCs to account for issues such as timescales of environmental variation and organismal responses. Quantifying TPCs as well as thermal tolerances is also important.

5.2. Leveraging Both Classic and Emerging Genetic Approaches

Evolution is likely to be important in understanding and projecting responses to climate variability and extremes, and models of thermal sensitivity increasingly incorporate selection and evolution. Classic approaches including common garden, reciprocal transplant, and heritability experiments are needed to inform models and address issues such as whether quantitative genetic models are appropriate for modeling the evolution of thermal sensitivity. At the same time, there are great opportunities to apply emerging genomic and other -omic approaches to the evolution of thermal sensitivity (Capblancq et al. 2020). But application of genomic approaches should be informed by existing quantitative approaches to predicting evolution (Shaw 2019). As sequencing costs decline, approaches such as evolve and resequencing incorporating experimental evolution are likely to be particularly insightful (Exposito-Alonso et al. 2019). Such experiments and associated models can help address issues such as the interplay of plasticity and evolution of thermal sensitivity and the occurrence of maladaptation of thermal sensitivity when organisms experience novel selection (Capblancq et al. 2020).

5.3. Expanding Beyond Thermal Sensitivity to Additional and Multiple Environmental Conditions

Now that a framework for the evolution of thermal sensitivity is reasonably well developed, opportunity abounds to extend the framework from thermal variability to variability in conditions such as drought and water availability, salinity, pH, and oxygenation. The promise of extending this approach is demonstrated by studies of how annual herbs in the genus *Lasthenia* respond to spatial and temporal variation in water availability within vernal pool grasslands. This research has found that plants from more consistently wet environments are more sensitive to dry conditions and that extreme drought events play a strong role in TPC evolution (Tittes et al. 2019). Additionally, expanding the framework to multiple stressors such as temperature plus water availability or pH is central to anticipating responses to climate change. Further consideration of how TPCs are altered by additional global change factors such as resource availability is also needed (Huey & Kingsolver 2019).

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Errata

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